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THE EFFECTS OF CROWDING AND MECHANICAL STIMULATION
ON WING MORPHOGENESIS IN MYZUS PERSICAE SULZ. (APHIDIDAE;
HOMOPTERA)

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "The effects of crowding and mechanical stimulation on wing morphogenesis in Myzus persicae Sulz. (Aphididae; Homoptera)" submitted by Walter Jerry Awram in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Adult, apterous aphids, Myzus persicae Sulz., were raised on discs of radish and cabbage leaves to determine the effect of different population densities on the proportion of alate offspring produced. Parents in the higher density treatments produced a greater proportion of alate offspring. It is thought that this was a result of the crowding of the young instars as well as the crowding of the parents. Parents fed on cabbage produced a greater proportion of alate offspring than did those on radish. The fecundity of the adults and the survival of the offspring were reduced when fed on cabbage.

Stroking was attempted to imitate the effects of crowding. Stroking the dorsal surfaces of the head, thorax, fore and hind abdomen, sides of the abdomen, antennae, and legs of adult apterae did not cause an increased proportion of alatae among their offspring. A slight response of questionable significance to stroking over the general dorsal surface was obtained. A small number of first and second instar larvae were stroked. None became alate.

Temporarily starving and crowding young adult apterae did not cause them to produce more than a normal number of alate offspring. First instar larvae were crowded. If their parents had not been crowded, most developed into apterae. If their parents had been crowded, most became alatae.

First and possibly second instar larvae are indeterminate, that is, can be switched toward the apterous state in the clone studied.

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1.0 Introduction

1.1 Life history

Aphids display an alternation of generations. During the course of a complete aphid life history various forms appear, are dominant for a short time, and then are succeeded by other forms. Although the variations on the main theme are great, a very generalized life history follows a pattern like this (Theobald 1926, Hottes and Frison 1931, Palmer 1952, Bodenheimer and Swirski 1957): in the spring a stem mother, or fundatrix, hatches from an egg which has overwintered on a host plant. The stem mother gives parthenogenetic birth to female individuals known as virginoparae. The virginoparae make their way to other host plants of the same species or to herbaceous, secondary hosts. These virginoparae give birth to other virginoparae, some which have wings and some which have no wings. This part of the cycle continues through the growing season. In the fall winged or unwinged sexuparae appear, forms capable of giving birth to both males and females. The males and the female offspring (oviparae) of the sexuparae return to a primary host, where they mate and produce an egg. The egg overwinters and the cycle begins again in the spring.

The factors which cause this amazing, clockwork-like succession of forms have long puzzled biologists. One of these factors, intraspecific interaction as a cause of wing formation,

is the subject of this thesis.

1. 2 Literature survey

Aphid polymorphism has been known for many years. Both Leeuwenhoek in 1695 and Reaumur (1737) recognized the apparent lack of males and assumed that aphids were hermaphroditic animals. Positive recognition of their parthenogenetic mode of reproduction was first made in 1748 by C. Bonnet. Bonnet also observed that eggs as well as larvae occurred. DeGeer in 1771 realized that the mothers (virginoparae) of larvae were quite different from the mothers (oviparae) of eggs. The next major form to be discovered in the cycle of polymorphism was the alate virginopara, whose position was first properly placed in the cycle by Kyber in 1815. Bonnemaïson (1951) cites these and other early references.

The various important stages in the life history of aphids have been known for 150 years. However, it is only within the last few years that the unravelling of the environmental factors inducing the production of the different forms has begun.

The appearance in the fall of sexual forms, both males and females, coincides with the onset of short periods of light and longer, alternate, periods of darkness. Marcovitch (1924) performed the first definitive experiments illustrating response to short photoperiods. This first effort has been substantiated by others since then, and lately Lees (1959, 1964), in a set of very elegant experiments, has shown that the stimulus is received by the median part of the brain of the mother aphid and then

transmitted to her embryos. In a very recent paper (1965), Lees has demonstrated that it is the increasing length of the dark period rather than the shortening of the day period that stimulates the aphid.

Studies directed at elucidating the cause(s) of the appearance of the winged forms^{have} been less successful. A factor which may have confused these studies is that there is more than one type of winged form. In addition to the most common form, the alate virginoparae, most male aphids are winged (a few are not and in some species both forms are possible) and in some species the oviparae also have wings. Therefore, experiments performed before the conditions evoking sexuals were known and controllable, may have been confounded by mistaking some or other of these forms. Whatever the case, there is certainly a large amount of conflicting data in the work reported thus far.

A number of workers (reviewed in Bonnemaison 1951) have supposed that a nutritional deficiency is a factor in the production of alate virginoparae. Mordvilko in 1907 supported this line of reasoning by observing that alatae were most common on wilted and dying plants. Tannreuther in 1907 thought that alate forms occurred on healthy plants. Baker and Turner (1916) observed that alatae arose on both young, healthy plants and on old plants offering little nutriment. Johnson and Birks (1960) stated that the condition of the host plant is one of two principal exogenous factors which influence alate formation; mature leaves favored

the production of alatae. According to Evans (1938), wing formation is negatively correlated with the protein content of the host plant, cabbage.

Another hypothesis with its proponents and dissenters was the "salts" theory. It was thought that excess concentrations of various inorganic salts caused the development of alatae (reviewed in Bonnemaïson 1951).

Humidity and other water relationships have been proposed as factors inducing wing formation. Rivnay (1937) reported that any condition which deprived aphids of adequate moisture caused them to produce winged forms. He said that low humidity, wilted plants, and periods of starvation are such conditions. Schaefer (1938) had a similar idea. He supposed that the concentration of the body contents of the parent caused alate offspring. Ackerman (1926) found four kinds of globules in the hemolymph and thought that changes in the proportion or concentration of these globules might control wing formation.

A factor which received considerable attention was the effect of temperature. Practically all of the temperatures within the range that aphids can endure have been singled out as being most favorable for wing formation (reviewed by Bonnemaïson 1951). Since Bonnemaïson's publication, Kenton (1955), Johnson and Birks (1960), and MacGillivray and Anderson (1964) have added to the list of temperatures optimum for alate production. Among these papers there is unanimity that near the highest temperatures which

can be survived (about 30 C.), only wingless virginoparae are produced.

Another possibility which was widely considered is the effect of photoperiod. Shull contributed most to this aspect of the problem. Many of his papers are reviewed by MacGillivray and Anderson (1964). The many interactions and combinations among various temperatures and other conditions make Shull's conclusions difficult to follow.

Intrinsic determination of wings has been hypothesized, especially in aphids which migrate between primary and secondary hosts. Bonnemaïson (1951), and MacGillivray and Anderson (1964) reported that alate mothers very rarely give birth to alate offspring. Yet Haviland (1921) observed that when the alate mothers remained on the host plant on which they were born, half their progeny were winged. Shull (1932) reported that each of 5 different clones of the same species (Macrosiphum solanifolii = euphorbiae Thomas) had characteristic and different degrees of alate production.

The most convincing factor thus far proposed has arisen from early reports in which alate formation was observed to be associated with dense populations (Wadley 1923). In his extensive study, Bonnemaïson (1951) calls this factor the "effet de groupe". He concluded that substantially larger numbers of alatae were produced when their parents were subjected to a high degree of crowding. He also suggested that crowding the young instars could cause them to develop wings. MacGillivray and Anderson (1958) reported

that the development of wings in Macrosiphum euphorbiae Thomas was not a response to crowding. Myzus persicae Sulz. raised concurrently under the same conditions did not develop winged forms. Lees (1959) suppressed alate production by raising Megoura viciae Buckton individually. In 1961 he reported that individually raised apterae which were producing only apterous offspring, produced alate offspring if they were crowded together in a testtube for 24 hours. Johnson (1965) presented very substantial evidence that contact between two adults of Aphis craccivora Koch caused them to produce winged offspring. He concluded that mechanical rather than visual or olfactory contact effected the response. The dorsal rather than the ventral surface of the parent aphid was affected by the stimulus. Aphids kept together for periods of time as short as 1 minute produced alate larvae. Most of the parents which responded did so completely, that is, their offspring were all alate. Johnson attempted to effect an artificial mechanical stimulus by stroking adult aptera for 2 minutes with a brush. Aphids so treated produced a percentage of alate offspring intermediate between that of singly reared parents and parents which had been in physical contact with other adults.

1.3 General objective

The original intention was to attempt to produce alate offspring by mechanically stimulating (stroking) their apterous parents. The purpose was to determine whether the essential, func-

tional component of the "effet de groupe" was the physical contact among the crowded adult aphids. Concurrent with efforts to mechanically induce the production of alatae, adult apterae were raised under different degrees of crowding to insure that the particular clone studied responded to crowding by producing alate offspring. The results of the first few experiments forced a broadening of the basis of the general objective, which then became an investigation of the effects of intraspecific interaction on the development of wings in the aphid Myzus persicae Sulz.

2.0 Methods and materials - general

The species studied was Myzus persicae (Sulz.). A clone was begun in early December 1964 with a single apterous virginopara taken from a radish plant in a greenhouse. The descendants of this individual were raised in a plywood cabinet, in a constant temperature room at 60 F. From March 1965 a Sherer Gro Lab growth chamber was used.

The aphids were reared on discs of radish leaf cut with an 18 mm cork borer. The discs were placed, dorsal surface down, on a column of wet cotton wool in a short glass tube. The aphids were contained on the surface of the disc by means of a small cylindrical glass cage. An elastic band was looped over the cage and under the glass tube. The elastic band secured the cage and also pressed the disc of radish into the cotton wool and ensured contact between the disc and the water in the wool.

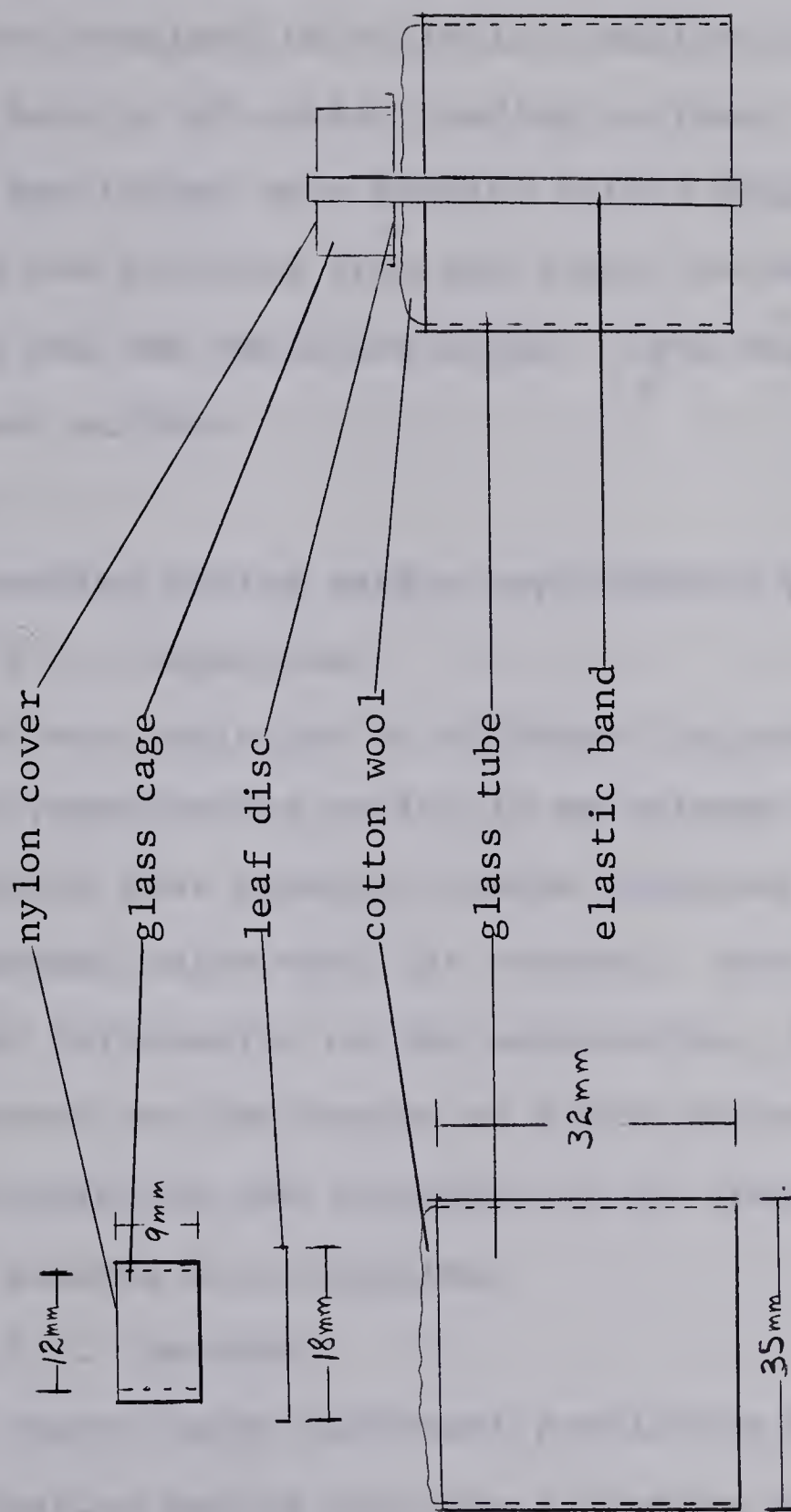
The glass tubes were placed in distilled water, in an aluminum tray. Each cage was 12 mm inside diameter and 9 mm high, enclosing an area on the leaf of 113.1 mm²; the glass tube which supported the cotton wool was 35 mm in diameter and 32 mm high. Circles, cut from a nylon material (27 strands per mm), were glued with LePage's Pliobond to the tops of the glass cages. Both cages and tubes were cut with a rotary carborundum saw. The 220 units, which were sufficient for the experiments done, were cut and assembled in less than 2 days. Fig. 1 illustrates the components of the assembled cage.

Each cage was identified by numbering with grease pencilling on the glass tube. At the end of each experiment, both cages and tubes were washed and the tubes were refilled with fresh cotton wool.

The discs were cut from radish plants, variety Forcing Scarlet Globe, grown under natural lighting conditions during the summer. In the fall and winter supplemental artificial light was added to bring the photoperiod to 14 hours. Only vigorous, growing leaves were used.

The photoperiod in the growth chamber was set at a constant 16 hours light per 24 hours for all the experiments. The temperature was set at 72 F. for 16 hours and 55 F. for the remaining 8 hours. The 16 hours at 72 F. began 1 hour after the lights were switched on. The growth chamber malfunctioned twice during the series of experiments. Both times, conditions

Fig. 1 Rearing Cage



were restored to normal within a few hours.

The leaf discs remained in suitable condition for 4-7 days, depending on the density of aphids feeding on them.

Both adults and larvae were handled with a moist camel hair brush. The brush was inserted from the front, between the front legs of the aphid and the aphid was moved. Care was taken to avoid touching the dorsal surface.

3.0 Experiments

3.1 Crowding during entire reproductive period

3.1.1. Objective

Adult aphids were subjected to different degrees of crowding during the entire reproductive period in an attempt to confirm Bonnemaïson's results that crowded parents produced more alate offspring than parents which were not crowded. Such treatment would also provide information on the association, if any, between the age of the parent and the degree of alate production, and on the effects of crowding on the fecundity of the parents and on the survival rate of parents and offspring.

3.1.2. Methods

Aphids were reared under different population densities for the entire reproductive period with the following conditions prevailing. The aphids chosen as parents came from leaf discs on which there were fewer than 10 individuals. All selected were in the fourth instar. When larviposition began, the parents were moved to new discs whenever the number of offspring exceeded 7. An attempt was made to limit the greatest number of offspring

per disc to 15. As a result, parents in the greater density treatments were moved more often than those under less dense conditions. The parents in the less dense treatments were deliberately picked up and put down in an attempt to equalize, across all treatments, the number of times parents were disturbed. The offspring were raised to maturity and the form of each, alate or apterous, was noted. A few intermediate forms were born. These were classed as alate.

4 experiments in which parents were crowded during the entire reproductive period were performed. The aphids for experiment 3 were selected from among the last offspring of experiment 2. These were kept within the treatments and replication of the parents. Experiment 4 contained treatments in which cabbage was used as a host plant as well as radish.

3.1.3. Results and discussion

The data from all experiments were analyzed by means of an IBM 7040 computer, program number BMD02V, which is an analysis of variance for factorial design. The death of individual aphids resulted in some missing values. Where there was one missing value in an experiment, an empirical value was substituted, calculated by the missing plots method of Goulden (1960). The experiments in which these calculations were made are appropriately footnoted in the tables. The calculations were necessary because the IBM program would not accept data with unequal subclass numbers.

The results of experiment 1 (table 1) confirmed the findings

of Bonnemaïson (1951). The difference between treatments in percent alate was highly significant. The more crowded the parents, the greater was the proportion of alate offspring. The results of the intermediate density (4 parents) were closer to the 8 parent treatment than to the 1 parent control treatment. The increased proportion of alatae was a result of both an increase in the number of alatae born and a decrease in the number of aptera born in the higher density. The increase in alate offspring did not manifest itself statistically until after the first third of the reproductive period, although the tendency appeared earlier. The length of the reproductive period was much the same across all treatments, averaging 21 days. The fecundity of the parents was unaffected by the increased population density, according to the statistical analysis. However, the number 3 replicate of the control group was not a normal individual and perhaps should not have been included in the analysis. It produced 21 offspring. The treatment average of 61.2. Aside from this single value, there was no overlap between treatments. The single parents produced more offspring per parent than the 4 parents, and these more than the 8 parents. The total offspring per parent per day did not show a statistical difference between treatments, but the trend toward decreasing numbers of offspring with increasing parent population density was apparent.

In experiment 1, it seemed that a population density of 4 parents was sufficient to produce the desired effect, therefore,

Table 1
Number of offspring born to apterous adults raised singly or in groups of 4 or 8 (Experiment 1)

Division of reproductive period of parents	Number of alate offspring per parent			total	Number of apterous offspring per parent			total	Length of reproductive period (days)	Total offspring reaching maturity	Total offspring per day	% alate
	first 1/3	middle 1/3	last 1/3		first 1/3	middle 1/3	last 1/3					
Grand mean all treatments	7.8	11.6	4.4	23.8	9.2	14.0	7.4	30.3	21.0	54.2	2.6	47.7
Treatment A (1 parent)	4.0 2-7	3.0 1-6	1.2 0-3	8.2 3-14	16.5 2-28	27.5 10-37	9.0 3-15	53.0 15-77	20.0 18-23	61.2 21-80	3.1 1-4	16.4 4-29
Treatment B (4 parents)	10.2 6-14	17.5 15-20	4.2 2-6	32.0 25-38	8.0 5-14	9.2 7-11	7.8 5-10	24.8 18-32	21.8 21-23	56.8 51-64	2.6 2-3	56.6 44-64
Treatment C (8 parents)	9.2 8-11	14.2 12-19	7.8 4-10	31.2 27-34	3.0 1-4	5.2 4-7	5.5 5-6	13.2 10-16	21.2 17-23	44.5 40-48	2.1 2-3	70.0 66-78
F	4.07	30.55	15.24	64.46	5.63	11.31	<1	7.38	<1	<1	<1	101.16

* P .05 ** P .01 \bar{X} mean R range

4 replicates in each treatment

TABLE 1. Results of the investigation of the effect of the concentration of the active substance on the rate of the reaction.

Concentration of the active substance, %	Time, min	Rate of the reaction, %/min	Rate of the reaction, %/min	Rate of the reaction, %/min	Rate of the reaction, %/min
0.1	10	1.0	1.0	1.0	1.0
0.2	10	2.0	2.0	2.0	2.0
0.3	10	3.0	3.0	3.0	3.0
0.4	10	4.0	4.0	4.0	4.0
0.5	10	5.0	5.0	5.0	5.0
0.6	10	6.0	6.0	6.0	6.0
0.7	10	7.0	7.0	7.0	7.0
0.8	10	8.0	8.0	8.0	8.0
0.9	10	9.0	9.0	9.0	9.0
1.0	10	10.0	10.0	10.0	10.0

The results of the investigation show that the rate of the reaction increases with the increase of the concentration of the active substance. The rate of the reaction is directly proportional to the concentration of the active substance. The rate of the reaction is 1.0 %/min at 0.1 % concentration, 2.0 %/min at 0.2 % concentration, 3.0 %/min at 0.3 % concentration, 4.0 %/min at 0.4 % concentration, 5.0 %/min at 0.5 % concentration, 6.0 %/min at 0.6 % concentration, 7.0 %/min at 0.7 % concentration, 8.0 %/min at 0.8 % concentration, 9.0 %/min at 0.9 % concentration, and 10.0 %/min at 1.0 % concentration.

the 8 parent treatment was eliminated and a 2 parent treatment begun in experiment 2. The same general trend in the proportion of the total offspring which were winged, was observed. The highest parent population density (4 parents) produced the greatest proportion of alatae. The results in the intermediate treatment were closer to the control than to the highest density treatment (table 2). The increased proportion of alatae was caused more by an increase of alates than by a decrease in apterae. Unlike experiment 1 the increase of alatae was greatest in the first third of the reproductive period. The mean total number of offspring (56) was close to the mean of experiment 1 (54). However, in experiment 2 the single parent treatment was the least fecund. The additional data collected on the average number of offspring per cage provided two interesting observations. First, although the number born was highly variable, the percent survival was high, averaging 87 percent for the experiment. The treatments varied little from this mean. The second observation was the highly significant difference between treatments in the average number of offspring per cage for the first third of the reproductive period and for the total average. In both these parameters the higher density parent treatments had more offspring per cage.

Experiment 2 was continued for a second generation as experiment 3. Unfortunately 2 of the control parents (raised alone) died soon after the experiment was begun. Analyses of variance were done using a desk calculator. In response to the observation on the

Table 2 Experiment 2

Number of alate and apterous offspring and average number of offspring per cage born to apterous parents raised singly or in groups of 2 or 4

Division of re-productive per- of parents	Number of alate offspring			Number of apterous offspring			Total offspring reaching maturity	Total offspring per cage last	Average number of offspring per cage			Total offspring born	% survival			
	first 1/3	middle 1/3	last 1/3	total	first 1/3	middle 1/3			last 1/3	first	middle			total		
Grand mean all treatments	6.6	7.2	3.4	17.1	14.1	11.1	13.8	39.2	56.1	29.4	16.3	17.9	12.8	15.5	63.8	87.0
Treatment A (1 parent)	0.8 0-3	2.5 0-8	3.0 0-6	6.2 3-9	15.8 9-23	12.2 6-22	14.5 8-23	42.5 27-62	48.8 35-65	14.9 5-23	11.2 9-12	16.5 13-25	12.8 10-15	13.2 11-14	56.2 41-70	86.0 78-93
Treatment B (2 parents)	6.2 1-13	9.2 2-18	3.5 1-6	18.5 7-31	16.2 11-22	11.2 7-14	15.5 7-24	42.8 28-56	61.0 35-85	27.3 15-40	13.8 11-19	16.2 12-19	12.5 11-14	14.2 13-16	69.2 44-90	86.8 80-94
Treatment C (4 parents)	12.8 11-16	10.0 5-15	3.8 0-7	26.5 22-32	11.2 6-17	9.8 7-12	11.5 3-18	32.5 21-44	58.5 42-76	46.2 38-52	24.0 23-25	21.0 18-22	13.2 9-17	19.0 18-20	66.0 48-81	88.3 86-94
F	13.25**	1.90	<1	6.37*	3.00	<1	1.59	2.83	1.93	8.13*	34.78**	3.66	<1	31.72**	2.29	<1

average number of offspring per cage made in experiment 2, great care was taken to keep the size of the offspring groups fairly small. Otherwise conditions were identical with those of experiment 2. The results of experiment 3 are given in table 3. The total number born per parent was even more variable than in experiment 2, but the average was similar. The percent survival was high and showed little variation, as in experiment 2. However, the percent alatae results differed from both experiments 2 and 1. The percent alatae did not increase with increased parent population density. There was no statistical difference between the single parent treatment and the 4 parent treatment. Very few more alate offspring were born to the crowded parents than to the parents raised singly. 2 explanations of the contradiction in the results of the proportions of alatae between experiments 1 and 2, and 3 are possible. The results of experiment 3 might be the result of a "generation" effect. It is possible that the environment experienced by the grandparent (parents in experiment 2) affected the progeny of experiment 3. The phenomenon which makes such a situation possible is the telescoping of generations characteristic of aphids. Very often, the more mature embryos in a parent have within themselves developing embryos. Lees (1959) has shown that such a "generation" effect is possible in the production of sexuals. However, I do not think the "generation" effect is a satisfactory explanation in this case. If the stimulus which diverts an embryo toward becoming apterous also diverts embryos which it contains, then a first generation of aptera

Table 3 Experiment 3

Number of alate and apterous offspring and average number of offspring per cage born to apterous parents raised singly or in groups of 2 or 4

Division of re-productive per-of parents	Number of alate offspring			Number of apterous offspring			Total offspring reaching maturity	% alate	Average number of offspring per cage			Total offspring born	% survival
	first	middle	last	first	middle	last			first	middle	last		
Grand mean all treatments	1.7	1.3	0.6	1.3	1.3	1/3	45.3	8.5	11.1	12.8	11.2	51.7	87.5
Treatment A (1 parent)	1.0	0.5	1.5	14.0	11.0	11.5	39.5	9.6	10.5	10.0	8.5	42.0	93.8
Treatment B (2 parents)	0.5	0.5	0.2	13.0	13.2	10.5	38.2	4.2	10.2	11.8	12.0	45.2	84.4
Treatment C (4 parents)	3.2	2.5	0.5	18.8	19.2	11.0	55.2	12.2	12.2	15.2	11.8	63.0	87.4
F							0.73	2.79				3.40	

would always have to be followed by a second generation of aptera. This is not so. Also, although the conditions under which the grandparents were kept as adults differed, the parents were raised to maturity under very similar conditions, i.e. between 5 and 10 individuals per radish disc.

A better explanation is the one suggested earlier from the results of experiment 2. The size of the offspring group might have an effect on the number of larvae within that offspring group which developed wings. Very few of the offspring groups in experiment 3 exceeded 15. A χ^2 test (Goulden 1960) was performed testing the independence of size class of offspring groups, and the number of alatae and apterae in each offspring group. The results are given in table 4. In experiment 2 there was a marked association between a large offspring group and alatae, and a corresponding association between a small offspring group and apterae. There were no such associations in experiment 3.

If the association between a high proportion of alatae and a high larval population density is valid, then perhaps the initial premise that high parent population density is the sole cause of alate production is incorrect. That is, the postnatal environment rather than the prenatal environment with respect to crowding may be the more important. The lack of association between a high percentage of alates and a high larval population density in experiment 3 could be interpreted as a threshold response. In other words it may take more than 10-15 larvae to make a crowd.

Table 4

χ^2 Test for independence between the average number of offspring per cage and the form of the offspring

	Average number offspring per cage	Number Apterous		Number Alate		O-T	(O-T) T
		O	T	O	T		
Experi- ment 2	10	47	33	5	19	14	5.9
	10-15	424	335	105	194	14	10.9
	15	564	667	490	387	89	23.6
						89	40.8
						103	15.9
						103	27.4**
							$\chi^2=123.9$
Experi- ment 3	10	154	151	14	17	3	.06
	10-15	707	703	76	80	3	.53
	15	281	288	40	33	4	.02
						4	.20
						7	.17
						7	1.48
							$\chi^2=2.46$
Experi- ment 4	15	730	629	292	393	101	16.22
	15-20	481	521	360	326	101	25.96
	20	424	491	375	308	34	2.22
						34	3.55
						67	9.14
						67	14.57**
							$\chi^2=71.66$
Experi- ment 4	10	140	105	34	69	35	11.67
	10-15	675	613	337	399	35	17.75
	15	802	898	680	584	62	6.27
						62	9.63
						96	10.26
						96	15.78
							$\chi^2=71.36$ **

O = observed T = theoretical

** = P < .01

Bonnemaison reported that Myzus persicae raised on radish produced more alatae than M. persicae raised on cabbage. If the hypothesis that alatae are a result of mechanical stimulation is correct, then there is an implication that aphids raised on radish are more restless than aphids raised on cabbage i. e. that on cabbage there is less intraspecific interaction. Another implication is that singly raised aphids, whether on radish or cabbage, should give birth to few alate offspring. Experiment 4 was performed with these considerations in mind. The results, given in table 5, were quite variable; however these observations could be made. In the radish treatments (A, C, E), the general pattern of results was similar to experiments 1 and 2. The greater the population density of the parents, the greater was the proportion of winged offspring. Again the increased proportion of alatae was a result of both an increase in alatae and a decrease in apterae in the high density treatment. The cabbage treatments (B, D, F) gave similar results with respect to the proportion of alatae, except that the intermediate treatment was closer to (exceeded) the high density treatment than to the control treatment.

Bonnemaison's observations with respect to host plant were not confirmed. In fact, the opposite result was obtained. Both the 2 and 4 parent treatments on cabbage had a greater proportion of alatae than the corresponding radish treatments. The hypothesis that intraspecific interaction maintains alate production is not disproved. The effects of radish vs cabbage are just reversed. That cabbage

Table 5 Experiment 4

Number of alate and apterous offspring and average number of offspring per cage born to apterous parents raised singly or in groups of 2 or 4 on radish or cabbage

Division of re-productive per- of parents	Number of 		
--	---	--	--

was a less desirable host plant could not be doubted. The percent survival on radish was characteristically high at 91.2 as compared to 71.7 on cabbage. The fecundity of the parents was also affected. The number born was less on cabbage than on radish. Cabbage would presumably result in restless aphids, there would be greater intraspecific interaction and thus a greater percentage of winged individuals.

Another χ^2 test for independence was performed on the data of experiment 4. The results are given in table 4. Again an association between a high proportion of alatae and a high larval population density was indicated.

3.2 Stroking

3.2.1. Objective

One of the more obvious effects of crowding is increased physical contact among the individuals crowded. The mechanical stimulation resulting from this increased contact might be involved in wing morphogenesis. If mechanical stimulation is the principal factor eliciting the production of alatae, then stroking the adults and/or the early instar larvae should produce winged forms. Aphids were stroked at various frequencies, over the entire dorsum and over particular parts of the dorsum to determine if alate production could be so induced (or more properly if apterae production could be reduced). It was hoped also to find out if some particular area was more sensitive to mechanical stimulation than others.

3.2.2. Methods

a. Adults. Fourth instar larvae were removed from offspring groups of 10 or fewer individuals and confined alone in separate

cages on radish discs. Stroking began after they had moulted into the adult but before they had offspring, or on the first day that offspring were born. They were stroked at different frequencies, usually once a day, with either the leg of an adult, apterous aphid, a Drosophila leg, or a human hair. The direction of stroking was more or less caudad, with the tarsal claws raked over the area being stroked. All of the legs were used. The aphid and Drosophila legs and the hair were manipulated with fine forceps under X12 power of a stereo binocular microscope. Some treatments consisted of timed contact with a live adult aphid which had been mounted on a pin with paraffin. The parent aphids were moved when their offspring numbered more than 7, usually every second day. In experiment 5 only, parents were moved almost daily.

b. Larvae. First and second instar larvae were stroked at different frequencies with a detached aphid leg. Larvae so treated were of 2 types, either from crowded or from uncrowded parents. They were removed from the parent within 8 hours of birth and raised to maturity alone.

The stroking experiments are listed and described in tables 6 and 7.

3.2.3. Results and discussion

a. Adults. As can be seen from table 8, parents in treatment C gave birth to a proportion of alate offspring much greater than that of the other treatments. Treatment C was the stroking

Table 6

Frequency of stroking, method of stroking and the area to which stroking was applied in experiments 5, 6, 7, 8, and 9

Experiment number	Number of replicates	List of treatments	Number strokes daily	Stroking device or method	Area to which stroking applied
5	4	A	100	hair	entire dorsum
	4	B	100	<u>Drosophila</u> leg	entire dorsum
	4	C	100	adult aphid leg	entire dorsum
	4	D	0		
6	4	A	0		
	4	B	for 2 mins.	live adult aphid	entire dorsum
	4	C	300	leg of adult aphid	entire dorsum
	4	D	300	hair	entire dorsum
7	4	A	500	leg of adult aphid	head
	4	B	500	leg of adult aphid	thorax
	3 ^m	C	500	leg of adult aphid	abdomen
	4	D	0		
8	4	A	400	leg of adult aphid	hind part of abdomen
	4	B	400	leg of adult aphid	fore part of abdomen
	4	C	400	leg of adult aphid	legs
	3 ^m	D	0		
9	4	A	0		
	4	B	500	leg of adult aphid	antennae
	4	C	500	leg of adult aphid	sides of abdomen
	3 ^m	D	500	hair	entire dorsum

^m = missing values

Table 7

Frequency of stroking, method of stroking and the area to which stroking was applied in experiments 10, 11, 12, 13, and 14

Experiment number	Number of replicates	List of treatments	Description and frequency of treatment
10	4	A	1000 strokes with aphid leg daily
	4	B	5 mins. contact with live aphid daily
	4	C	smeared with cornicle secretion twice daily
	4	D	control
11	5	A	control
	4	B	500 strokes once in first instar
	4	C	500 strokes once in first instar; once in second instar
12	3	A	control
	3	B	500 strokes once in first instar
	3	C	500 strokes once in first instar; once in second instar
13	4	A	200 strokes 3 times during first instar
	3	B	200 strokes 3 times during second instar
	2	C	200 strokes 3 times during first and second instars
	6	D	control
14	3	A	control
	3	B	300 strokes once during first instar
	4	C	300 strokes twice during first instar
	4	D	300 strokes once during first; once in second instar
	4	E	300 strokes once in first instar; twice in second instar

All stroking applied to entire dorsum.

Table 8 Experiment 5

Number of alate and apterous offspring born to aptera stroked 100 times daily with a hair, a <u>Drosophila</u> leg, or an aphid leg									
Division of re-productive period of parent	Number of alate offspring first middle last total			Number of apterous offspring first middle last total			Total offspring reaching maturity	% alatae	
	1/3	1/3	1/3	1/3	1/3	1/3			
Grand mean all treatments	1.1	3.8	4.1	9.0	12.4	12.3	14.0	38.7	47.7 18.8
Treatment A \bar{X} 100 strokes hair	1.5	1.5	3.5	6.5	14.0	16.0	15.2	45.2	51.8 9.8
R	0-2	1-3	0-10	0-13	2-25	1-28	3-28	6-71	6-78 0-20
Treatment B \bar{X} 100 strokes <u>Drosophila</u> leg	1.2	2.0	1.8	5.0	11.0	12.5	14.0	37.5	42.5 9.6
R	0-5	0-7	0-6	1-13	6-21	4-27	8-22	22-50	23-63 3-21
Treatment C \bar{X} 100 strokes aphid leg	0.2	7.0	9.5	16.8	9.2	7.4	11.5	28.2	45.0 41.4
R	0-1	4-11	1-13	7-25	2-16	3-15	3-25	8-56	15-74 24-52
Treatment D \bar{X} control	1.5	4.8	1.5	7.8	15.2	13.2	15.2	43.8	51.5 14.3
R	0-4	0-10	1-2	2-12	8-22	7-21	5-27	20-57	22-68 9-22
F	<1	2.99	5.90	7.93	1.02	<1	<1	<1	<1 14.53

**

**

*

with the aphid leg. The higher percentage of alatae was a result more of increased alate births than of decreased apterous births. In the first third of the reproductive period, treatment C individuals had about the same number of alate offspring as individuals of the other treatments. By the last third, the increased incidence of alate offspring in treatment C was great enough to be of statistical significance. Production of apterous offspring was least in treatment C, although not significantly so. The length of the reproductive period was about the same for all treatments, averaging 12.8 days. The total offspring born during the experiment averaged 47.7 per parent. Variation from this mean was considerable.

On the basis of the apparent success of experiment 5, experiment 6 was begun. The results are given in table 9. The Drosophila leg was dropped as a stroking device because of its poor utility as such an instrument and because it seemed no more effective than the hair. The difference between treatments, with respect to proportion of alatae, narrowly missed statistical significance at $P < .05$. The treatments followed an order that would support the hypothesis that alatae are determined by intraspecific interaction. That is, the percentage of alatae was greatest in treatment B (live aphid), next in treatment C (aphid leg) next in treatment D (hair), and least in treatment A (control). The argument is further supported by the number of alatae and apterae in each treatment during each third of the

Table 9 Experiment 6

Number of alate and apterous offspring and average number of offspring per cage born to aptera stroked 300 times daily with an aphid leg or hair or kept in contact with a live aphid for 2 minutes

	Total number alate offspring	Total number apterous offspring	Total number offspring reaching maturity	% alate	Average number of offspring per cage	% survival
Grand mean all treatments	13.4	27.6	40.9	31.9	13.4	88.6
Treatment A \bar{X} (control) R	8.0 0-15	30.0 16-48	38.0 16-63	17.4 0-25	12.0 11-13	82.3 64-92
Treatment B \bar{X} (2 mins con- R tact live aphid)	19.0 9-29	20.2 13-26	39.2 22-53	46.1 37-56	12.5 11-14	96.0 93-100
Treatment C \bar{X} (300 strokes R aphid leg)	12.2 5-15	20.0 14-29	32.2 26-43	38.0 19-52	13.0 10-15	85.4 80-94
Treatment D \bar{X} (300 strokes R with hair)	14.2 9-23	40.0 32-56	54.2 44-68	26.3 18-38	16.2 15-17	90.8 88-94
F	1.33	3.93*	1.59	3.70	10.99**	3.85

* = P < .05 ** = P < .01

reproductive period. Treatment B parents had the most alate and second least apterous offspring; treatment A had the least alate and second most apterous offspring; treatment C was intermediate. The mean size of the offspring groups was greatest in treatment D, however D had the second lowest proportion of alate offspring. The rate of survival was characteristically high.

The frequency of stroking in experiment 6 was 3 times that of experiment 5, yet there was not a comparable increase in the effect which the stroking was presumed to induce. However, I viewed the results optimistically and proceeded as follows. If mechanical stimulation was the cause of alatae production, then perhaps there was some special area of the body most receptive to such stimulation. Experiments 7, 8, and 9 were performed to find out if any of the parts of the body listed in table 6 were particularly sensitive to mechanical stimulation. Concentration of stroking in a small area would also have the effect of increasing the intensity of the treatment. I hoped that the dorsal abdominal area would be a sensitive one because the often observed phenomenon of alatae giving birth only to apterae might then be explained. Receptors on the abdomen would be covered by the wings and could therefore not be stimulated.

The results (tables 10, 11 and 12) were rather disappointing. In both experiments 7 and 8, the control treatments had the highest proportion of alatae. In experiment 9, the control was the second

Table 10 Experiment 7

Number of alate and apterous offspring and average number of offspring per cage born to aptera stroked 500 times daily on the head, thorax, or abdomen						
	Total number alate offspring	Total number apterous offspring	Total number offspring reaching maturity	% alate	Average number of offspring per cage	% survival
Grand mean all treatments	3.4	28.1	30.2	10.9	9.2	83.6
Treatment A \bar{X} (500 strokes R head)	5.5 4-9	38.8 29-52	44.2 33-57	13.1 8-23	10.2 9-12	93.4 89-98
Treatment B \bar{X} (500 strokes R thorax)	1.5 0-2	28.0 11-47	29.5 13-49	6.6 0-15	9.0 7-10	77.7 46-100
Treatment C \bar{X} (500 strokes R abdomen)	3.2 0-10	23.8 8-47	22.0 1-57	8.7 0-18	7.8 5-11	82.5 71-92
Treatment D \bar{X} (control) R	3.2 2-4	21.8 6-30	25.0 8-33	15.4 9-25	9.8 8-13	80.8 50-100
F	1.53	2.53	2.68	1.05	2.83	< 1

Table 11 Experiment 8

Number of alate and apterous offspring and average number of offspring per cage born to aptera stroked 400 times daily on the abdomen or legs						
	Total number alate offspring	Total number apterous offspring	Total number offspring reaching maturity	% alate	Average number of offspring per cage	% survival
Grand mean all treatments	9.8	40.8	50.5	17.9	10.1	86.0
Treatment A \bar{X} (400 strokes R hind abd.)	7.0 2-11	48.0 35-56	55.0 37-68	12.0 5-16	10.5 9-12	87.5 82-96
Treatment B \bar{X} (400 strokes R fore abd.)	11.8 5-18	48.0 35-63	59.8 49-72	19.8 10-30	10.2 8-11	85.6 81-92
Treatment C \bar{X} (400 strokes R legs)	7.0 0-14	32.0 17-56	39.0 17-70	12.8 0-26	9.0 8-10	78.6 52-99
Treatment D \bar{X} (control) R	13.2 7-16	35.0 30-40	48.2 45-52	27.1 15-33	10.8 9-12	92.0 83-96
F	1.95	1.57	1.14	3.83	2.24	< 1

Table 12 Experiment 9

Number of alate and apterous offspring and average number of offspring per cage born to aptera stroked 500 times daily on the antennae or sides of the abdomen

	Total number alate offspring	Total number apterous offspring	Total number offspring reaching maturity	% alate	Average number of offspring per cage	% survival
Grand mean all treatments	19.2	51.1	70.3	28.0	15.8	94.3
Treatment A (control)	\bar{X} 23.5 R 15-32	46.8 43-50	70.2 58-82	32.9 26-39	17.2 14-19	94.3 90-97
Treatment B (500 strokes with antennae with aphid leg)	\bar{X} 18.2 R 12-28	39.8 15-54	58.0 27-75	33.5 18-44	15.5 14-16	96.6 93-100
Treatment C (500 strokes sides of abdomen)	\bar{X} 14.5 R 8-21	55.2 30-70	69.8 42-84	21.8 10-29	15.0 12-17	91.3 88-98
Treatment D (500 strokes dorsum with hair)	\bar{X} 20.8 R 10-33	62.5 55-70	83.2 76-92	24.0 13-38	15.2 14-16	94.9 93-96
F	1.11	3.57	4.60*	1.35	1.88	1.60

$$* = P .05$$

highest being slightly exceeded by the B treatment (500 strokes to the antennae). In none of the experiments was there any statistical difference of consequence in alate production. The percent alatae increased through the 3 experiments; 7 averaged 10.9, 8 17.9, and 9 28.0. There was a corresponding increase in the average size of the offspring group. A test was performed to determine if there was an association between the type of progeny and the size of the offspring groups. There was such an association in experiments 8 and 9. The results are given in table 13. The percent survival also displayed this trend, increasing through 7, 8, and 9.

The results of experiments 7, 8, and 9 caused me to doubt my original success with experiments 5 and 6. Experiment 10 was attempted to confirm or refute the results of experiments 5 and 6. The cornicle secretion treatment was introduced to round off the experiment to 4 treatments. Since it is possible that the intraspecific interaction is of a chemical as well as, or rather than, a mechanical nature, I thought it worth trying this most obvious secretion. Roughly handled aphids, which had secreted the cornicle exudate, were brushed against the individuals in the treatment. The cornicle secretion solidified almost immediately. By the end of the experiment, the treatment C parents were coated with the hardened secretion.

The results are given in table 14. The differences in the percent alatae were not statistically significant, but the

Table 13

χ^2 Test for independence between the average number of offspring per cage and the form of the offspring

	Average number offspring per cage	Number Apterous		Number Alate		O-T	(O-T) T
		O	T	O	T		
Experi- ment 7	10	149	144	13	18	5	.17
	10-15	264	270	40	34	5	1.39
	15	16	15	1	2	4	.06
						4	.47
						1	.07
						1	.50
							$\chi^2=2.66$
Experi- ment 8	10	212	198	32	46	14	.99
	10-15	330	347	98	81	14	4.26
	15	64	62	12	14	17	.83
						17	3.58
						2	.06
						2	.29
							$\chi^2=10.01^{**}$
Experi- ment 9	10	79	63	8	24	16	4.06
	10-15	227	195	43	75	16	10.67
	15	428	476	231	183	32	5.25
						32	13.67
						48	4.84
						48	12.59
							$\chi^2=51.08^{**}$

O = observed T = theoretical

Table 14 Experiment 10

Number of alate and apterous offspring and average number of offspring per cage born to aptera stroked 1000 times daily with an aphid leg, kept in daily contact with live aphid for 5 mins., or smeared with cornicle secretion twice daily							
	Total number alate offspring	Total number apterous offspring	Total number offspring reaching maturity	% alate	Average number of offspring per cage	% survival	
Grand mean all treatments	9.4	31.4	40.9	22.3	12.2	88.9	
Treatment A \bar{X} (1000 strokes dorsum)	10.8	29.8	40.5	24.4	11.5	92.4	
R	1-21	24-42	26-51	4-43	10-13	86-96	
Treatment B \bar{X} (5 mins. contact with live aphid)	16.2	27.0	43.2	37.4	13.2	90.1	
R	11-24	19-33	38-51	25-50	12-14	86-94	
Treatment C \bar{X} (cornicle secretion twice daily)	6.0	30.2	36.2	16.8	11.2	87.0	
R	2-12	22-39	28-43	6-31	9-14	68-98	
Treatment D \bar{X} (control)	4.8	38.8	43.5	10.5	12.8	86.0	
R	2-10	34-49	36-53	6-21	12-14	75-96	
F	2.78	2.52	< 1	2.71	2.30	< 1	

treatments rank in much the same order as in experiment 5 and 6 so far as these are comparable. Again the number of alatae and apterae corresponded to what would reasonably be expected. The whole aphid and stroking treatments had more alate offspring and less apterous offspring than the control. The control treatment D had the least alate and the most apterous offspring. Statistical significance was reached in the differences in apterous offspring in the second and third batches of offspring. The cornicle secretion treatment was ineffective.

Reasons for the conflicting results obtained in the stroking experiments were not obvious to me. There appeared to be a response to general stroking over the entire dorsal surface. I can offer no explanation as to why a stroking frequency of only 100 strokes per day should seem to be much more effective than 300 or 1000 strokes per day. The lack of response when stroking was restricted to particular areas implies that the sensitive area, if such an area exists, was missed. This seems unlikely because the areas chosen covered most of the dorsum.

b. Larvae. Because of the association that was revealed in experiments 1, 2, and 4 between a high proportion of alate offspring and a large sized offspring group, there was a basis for suspecting that in M. persicae, the postnatal environment may be of greater consequence than prenatal conditions. Experiments 11, 12, 13, and 14 which were attempts to test this suspicion are listed in table 7.

I have followed a general tendency to think in terms of establishing conditions that result in the production of alatae. It is more likely that as Johnson and Birks (1960) have stressed, one should think in terms of conditions that result in the production of apterae. The embryo probably begins its development toward an alate form. Along its developmental path, it encounters conditions which may keep it on the path to becoming alate or "switch" it into an apterous pathway. Such a switch may be irreversible. This means that conditions designed to maintain an embryo or larva on the alate path may be imposed in vain if that embryo or larva has already been switched to the apterous path. Experiments 11 and 12, the results of which appear in table 15, may have suffered from this oversight. Each experiment comprised the progeny of a single parent which had been raised under uncrowded conditions. The number of strokes per aphid (with an adult aphid leg) is given in table 8. None became alate. Experiments 13 and 14 did not suffer from this possible defect. The parents were under very crowded conditions ($17/50.3 \text{ mm}^2$) for 4 days before the experiments began. 3 of the parents were selected as parents for experiments 13 and 14. The offspring of these 3 parents were stroked at the frequencies given in table 7. None developed into alatae (table 16). The offspring, all apterae, were kept and the first 2 batches of their offspring were collected and raised to maturity. The results appear in tables 17 and 18 and are labelled as experiments 15 and 16. No third generation effects could be

Table 15

Adult form of larvae stroked during first and second instars

Experiment 11

Treatment	Treatment description	Replicate					
		1	2	3	4	5	6
A	200 strokes 3 times during 1st instar		Ap*		Ap	Ap	Ap
B	200 strokes 3 times during 2nd instars	Ap	Ap		Ap		
C	200 strokes 3 times during 1st and 2nd instars	Ap			Ap		
D	0 strokes (control)	Ap	Ap	Ap	Ap	Ap	Ap

Experiment 12

A	0 strokes (control)	Ap	Ap		Ap
B	300 strokes once during 1st instar	Ap		Ap	Ap
C	300 strokes twice during 1st instar	Ap	Ap	Ap	Ap
D	300 strokes once during 1st, once during 2nd instars	Ap	Ap	Ap	Ap
E	300 strokes once during 1st, twice during 2nd instars	Ap	Ap	Ap	Ap

* Ap = apterous, Blank indicates a death

Table 16

Adult form of larvae stroked during first and second instars

Experiment 13

Treatment	Treatment description	Replicate				
		1	2	3	4	5
A	0 strokes (control)	Ap	Ap	Ap	Ap	Ap
B	500 strokes 1st instar	Ap		Ap	Ap	Ap
C	500 strokes 1st and 2nd instars	Ap	Ap	Ap	Ap	Ap

Experiment 14

A	0 strokes (control)	Ap	Ap	Ap
B	500 strokes 1st instar	Ap	Ap	Ap
C	500 strokes 1st and 2nd instars	Ap	Ap	Ap

Ap = apterous, Blank indicates a death

Table 17 Experiment 15

Number of alate and apterous offspring and average number of offspring per cage born to aptera which had been stroked in first and second instars

	Total number alate offspring	Total number apterous offspring	Total number offspring reaching maturity	% alate	Average number of offspring per cage	% survival
Grand mean all treatments	13.8	16.3	30.1	46.1	15.8	93.6
Treatment A \bar{X} R	12.0 4-16	19.5 16-23	31.1 20-38	38.1	16.5 11-21	94.0 90-100
Treatment B \bar{X} R	17.8 6-26	12.5 8-17	30.2 23-34	58.9	16.5 14-18	91.2 82-97
Treatment C \bar{X} R	11.5 4-17	17.0 12-24	28.5 16-39	40.3	14.5 8-20	95.8 94-100
F	<1	3.62	<1		<1	1.41

1. Grandparents heavily crowded; treatment A - control; treatment B - parents stroked 500 times in first instar; treatment C - parents stroked 500 times in each of first and second instars.

Table 18 Experiment 16

Number of alate and apterous offspring and average number of offspring per cage born to aptera which had been stroked in first and second instars						
	Total number alate offspring	Total number apterous offspring	Total number offspring reaching maturity	% alate	Average number of offspring per cage	% survival
Grand mean all treatments	10.2	13.6	23.8	32.7	12.6	95.8
Treatment A \bar{X}	15.0	14.3	29.3	52.2	15.3	94.9
R	12-18	8-20	26-35	43-69	13-18	90-100
Treatment B \bar{X}	7.7	13.0	20.7	28.5	10.7	98.6
R	2-13	10-16	15-24	13-56	8-12	96-100
Treatment C \bar{X}	8.0	13.3	21.3	17.5	11.7	94.1
R	3-12	8-18	20-23	14-60	11-12	91-100
F	28.90**	< 1	7.13*	2.28	5.02	< 1

1. Grandparents heavily crowded; treatment A - control; treatment B - parents stroked 500 times in first instar; treatment C - parents stroked 500 times in each of first and second instars

* = P .05 ** = P .01

observed with respect to the proportion of alatae born.

3.3 Temporary crowding

3.3.1. Objective

a. Adult aphids were crowded at different densities, for different periods of time away from the host plant in an attempt to induce the production of alate forms. It was hoped to learn the smallest amount of "togetherness" which evoked a response.

b. First and second instar larvae were crowded for short periods to determine whether or not high postnatal population densities could maintain the larvae on the path to the alate condition.

3.3.2. Methods

a. Adult aphids were crowded in the standard sized cage previously described, and also in a small cage 8 mm in diameter and 9 mm high, enclosing an area on the leaf of 50.3 mm^2 , and in microtubes 4 mm in diameter and 7 mm long. They were maintained in these containers on moist cotton. No leaf discs were available to them during the period of their confinement. After a set period of time, they were placed on fresh leaf discs and kept individually. Their first 2 batches of offspring were raised to maturity and the form they had taken was noted. All other conditions were identical to those described in the general methods and materials section. Table 19 lists the treatments, the duration and the intensity of crowding in each of the

Table 19

Description of experiments 17, 18, 19, 20, 21

Experiment number	Number of replicates	List of treatments	Description of treatments
17	4 4 4	A B C	1 aphid kept in microtube overnight 4 aphids kept in microtube 1 hr. 4 aphids kept in microtube overnight
18*	4 4 3 ^m 3 ^m	A B C D	1 aphid kept away from host plant 1 hr. 1 aphid kept away from host plant 2 hrs. 1 aphid kept away from host plant 4 hrs. 1 aphid kept away from host plant 16 hrs.
19*	4 4 4 4	A B C D	2 aphids crowded together away from host plant 1 hr. 2 aphids crowded together away from host plant 2 hrs. 2 aphids crowded together away from host plant 4 hrs. 2 aphids crowded together away from host plant 16 hrs.
20*	4 4 4 4	A B C D	4 aphids crowded together away from host plant 1 hr. 4 aphids crowded together away from host plant 2 hrs. 4 aphids crowded together away from host plant 4 hrs. 4 aphids crowded together away from host plant 16 hrs.
21*	4 4 4 4	A B C D	16 aphids crowded together away from host plant 1 hr. 16 aphids crowded together away from host plant 2 hrs. 16 aphids crowded together away from host plant 4 hrs. 16 aphids crowded together away from host plant 16 hrs.

^m = missing values

* = crowded in large cage

experiments. The periods of crowding which lasted less the 16 hours were done during the day. The 16 hour periods included the 8 hours of night. Because of the lack of time and space, not all 16 of the aphids crowded 16 together could be used; 4 were selected to represent that treatment.

b. First instar larvae less than 12 to 24 hours old were crowded in the small cage for 12, 16, or 24 hours at densities of 16, 32, or 48, per 50.3 mm^2 . The parents were either crowded or uncrowded. A decription of these experiments (25, 26, 27) is given in table 27, page 57.

3.3.3. Results and discussion

a. Adults. The results which Lees (1961, Megoura viciae) and Johnson (1965, Aphis craccivora) reported with respect to the effect of temporary crowding were unequivocal. In M. viciae, individuals that had been producing essentially all apterous offspring switched completely to the production of essentially all alate offspring after they had been crowded for 24 hours. In A. craccivora, Johnson found that a similar reversal could occur after as little as 1 or 2 minutes contact between as few as 2 aphids. I tried similar temporary crowding in an effort to clarify the confusing results which I obtained in the rearing and stroking experiments. Experiments 17, 18, 19, 20, and 21 formed the basis of the temporary crowding experiments.

In experiment 17 (table 20) no difference in the proportion

Table 20 Experiment 17

Number of alate and apterous offspring and average number of offspring per cage born to aptera kept alone or 4 together in microtubes for 1 hr or overnight

	Number of alate offspring first batch		Number of apterous offspring first batch		Total offspring reaching maturity	% alate	Average number of offspring per first batch		% survival
Grand mean all treatments	4.8	17.1	8.6	37.6	54.7	31.3	15.3	12.7	86.0
Treatment A (1 aphid in microtube overnight)	5.8 3-9	11.8 4-20	5.5 4-7	28.2 20-36	40.0 24-55	29.5 17-36	14.5 9-19	11.0 9-13	74.0 52-84
Treatment B (4 aphids in microtube 1 hr)	6.0 4-7	23.8 17-33	10.2 6-13	42.0 33-56	65.8 50-77	36.2 27-45	17.8 14-21	13.8 10-16	94.3 89-96
Treatment C (4 aphids in microtube overnight)	2.8 1-4	15.8 10-25	10.0 7-12	42.5 32-55	58.2 50-68	27.1 15-37	13.8 9-17	13.2 11-15	89-6 82-94
F	5.66*	3.21	4.92*	3.90*	8.07*	1.19	1.70	2.25	7.17*

* = P < .05

of alate offspring among the treatments could be observed. The percent alatae was almost identical in the aphids kept individually, to those crowded together in a microtube. Treatment B (4 crowded for 1 hour) had the greatest proportion of alatae but the difference was not significant. The significantly high F values obtained for the first batch apterous, total offspring and total apterous were, I think, a result of the unusually small percent survival of treatment A.

Experiment 18 (table 21), like experiment 3, contained many missing values and could not be analyzed by means of the IBM program. Only the means are given. Experiment 18 was essentially a test of the effect of different periods of temporary starvation on the production of offspring. No pattern could be observed in any of the measurements taken. The number of alate offspring, the number of apterous offspring, the total number of offspring, the proportion of offspring which were alate, the total offspring born and the percent survival were not noticeably affected by 1, 2, 4, or 16 hours of starvation.

The results of experiment 19 (table 22) were similar to those of experiment 18. There appeared to be no association between the proportion of alatae produced and the length of time that 2 parent aphids were in the same cage with one another. The exception to this general observation was the number of alate offspring in the first batch. Significantly more alatae were born to individuals in treatment D (16 hours) than in

Table 21 Experiment 18

Number of alate and apterous offspring and average number of offspring per cage born to aptera starved alone for 1, 2, 4, or 16 hours						
	Total number alate offspring	Total number apterous offspring	Total number offspring reaching maturity	% alate	Average number of offspring per cage	% survival
Grand mean all treatments	6.9	18.4	25.3	25.6	15.6	81.0
Treatment A \bar{X} (alone 1 hr) R	2.8 1-5	16.2 10-29	19.0 12-32	16.9 6-31	13.0 10-17	71.3 55-94
Treatment B \bar{X} (alone 2 hrs) R	10.0 4-16	19.8 14-24	29.8 27-34	32.4 14-53	16.2 14-18	91.0 87-97
Treatment C \bar{X} (alone 4 hrs) R	6.0 5-8	16.7 15-19	22.7 20-24	26.4 20-33	14.7 13-17	80.0 59-92
Treatment D \bar{X} (alone 16 hrs)	9.0 2-15	21.3 16-24	30.3 26-34	28.5 8-48	19.0 16-22	81.5 79-84

Table 22 Experiment 19

Average number of offspring per cage and number of alate and apterous offspring born to aptera which had been crowded 2 together for 1, 2, 4, or 16 hours												
	Number of alate offspring			Number of apterous offspring			Total offspring reaching maturity	% alate	Average number of offspring per cage			% survival
	first batch	second batch	total	first batch	second batch	total			first batch	second batch	total	
Grand mean all treatments	4.0	1.6	5.6	9.1	9.2	18.4	23.9	22.4	15.4	12.7	15.1	85.5
Treatment A (2 crowded 1 hour)	2.0 1-4	1.5 0-2	3.5 2-6	9.2 2-16	6.5 1-13	15.8 6-29	19.2 9-35	22.1 13-33	14.0 7-25	8.2 1-15	11.0 5-20	86.4 69-100
Treatment B (2 crowded 2 hours)	1.0 1-2	2.5 0-4	3.5 1-6	10.8 5-15	7.0 0-12	17.8 5-27	21.2 6-33	16.1 13-18	12.5 6-18	10.0 0-17	12.0 6-18	90.9 81-100
Treatment C (2 crowded 4 hours)	4.8 0-11	0.2 0-1	5.0 0-11	11.2 10-14	3.8 0-8	15.0 11-18	20.0 11-25	20.8 0-44	20.5 11-27	7.5 0-10	17.5 11-27	76.2 67-100
Treatment D (2 crowded 16 hours)	8.2 5-11	2.0 0-5	10.2 5-16	5.2 1-12	19.8 14-24	25.0 15-36	35.2 31-41	30.6 12-52	14.8 13-17	25.0 22-28	20.0 18-22	88.5 80-100
F	6.66*	2.03	3.44	1.28	14.36**	1.29	2.93	1.05	1.40	13.14**	2.23	1.86

treatments A and B (1 and 2 hours). An intermediate number was born to the individuals in the intermediate treatment C (4 hours). The significant F values for the second batch of apterae was probably a result of the zero values for replicates 1 and 2 for treatment C. These would probably best be viewed as missing values. The significant F value for the size of the offspring group of the second batch also reflected the zero of replicate 2, treatment C. The high value for treatment D (size of offspring group) might be suspected as the cause of the high percent alatae of treatment D. However, the second batch in treatment D was almost all apterous.

A number of the parameters in experiment 20 (table 23) displayed statistically significant differences among the treatments. Most important of these was the percent alatae. The proportion of winged offspring (29 percent) was greatest in treatment D (16 hours). The percentage for treatment A (1 hour) was considerably less at 11 percent. Treatment B (2 hours) was intermediate (21 percent). However the pattern was broken by treatment C (4 hours) which had only 2.7 percent alatae. The situation was the same for alate offspring in the first batch and total alate offspring; treatment C falling outside the pattern. The difference between treatments shown by the number of apterous offspring in the second batch was a manifestation of the unusually high fecundity of the treatment D individuals. Treatment D had an average offspring group size in the second batch that was

Table 23 Experiment 20

Average number of offspring per cage and number of alate and apterous offspring born to aptera which had been crowded 4 together for 1, 2, 4, or 16 hours

	Number of alate offspring		Number of apterous offspring		Total offspring reaching maturity	% alate	Average number of offspring per cage		% survival		
	first batch	second batch	total	first batch			second batch	first batch		second batch	
Grand mean all treatments	4.0	1.9	5.9	12.8	25.6	31.4	15.9	19.8	15.6	17.7	88.6
Treatment A (4 crowded 1 hour)	2.8 1-4	0.8 0-2	3.5 1-5q	16.5 12-21	29.2 25-38	32.8 29-39	11.3 3-17	21.2 18-24	14.0 12-17	17.5 15-20	93.0 85-100
Tream B (4 crowded 2 hours)	3.8 1-10	3.2 0-6	7.0 2-16	16.0 8-24	22.8 12-37	29.8 15-53	20.6 11-30	22.8 10-38	9.8 5-18	16.2 8-28	93.8 80-100
Treatment C (4 crowded 4 hours)	0.6 0-1	0.0 0.5	0.5 0-1	11.2 7-14	9.2 8-11	20.5 15-23	2.7 0-7	17.0 14-23	11.0 9-13	14.2 11-16	75.3 55-100
Treatment D (4 crowded 16 hours)	9.0 3-11	3.5 1-6	12.5 5-16	7.2 3-9	22.5 16-30	29.8 24-39	28.8 17-40	18.0 14-23	27.5 21-34	22.8 18-27	92.3 81-100
F	7.07**	3.17	6.70*	3.79	13.92**	3.37	11.09**	< 1	13.34**	1.94	2.26

much higher than the other treatments. The large size of the offspring group was not associated with a corresponding increase in alatae.

Experiment 21 (table 24) completed the symmetry of the experimental design of the crowding experiments. There was no difference between treatments in the number of alatae or apterae produced or in the percent alatae. The significance attained with respect to total offspring, average and second day size of offspring group and the total born was caused by the partial sterility and low survival rate of the treatment C individuals.

The data obtained from experiments 18, 19, 20, and 21 contradicted some of the results obtained by Lees and Johnson. Several explanations are possible. Both these workers had raised the parent aphids used in their experiments separately. Mine were taken from groups of 10 or fewer individuals. The results I obtained may have been confounded by this previous association. Another explanation was that the density of parents was not great enough. It is possible that the 16 aphids would not encounter one another often enough to produce a response. A third explanation might be that the 4 individuals selected to represent the 16 of the high density treatments had never been walked upon, i. e. had themselves been the most active. Still another possible explanation is that I did not use enough replicates. Experiments 22, 23, and 24 were performed to correct these possible defects. Instead of 4 treatments only 2 were

Table 24 Experiment 21

Average number of offspring per cage and number of alate and apterous offspring born to aptera which had been crowded 16 together for 1, 2, 4, or 16 hours

	Number of alate offspring		Number of apterous offspring		Total offspring reaching maturity	% alate	Average number of offspring per cage		% survival
	first batch	second batch	first batch	second batch	total		first batch	second batch	total
Grand mean all treatments	3.4	3.8	7.2	10.4	8.7	19.1	26.3	25.7	16.7 13.9 15.4 81.7
Treatment A (16 crowded 1 hour)	\bar{X} 3.5 0-8	2.5 2-4	6.0 2-12	10.8 3-16	10.5 4-14	21.2 7-30	27.2 19-32	26.0 6-63	17.0 14.8 16.0 86.0 12-20 11-18 12-19 79-93
Treatment B (16 crowded 2 hours)	\bar{X} 4.0 0-11	4.0 0-10	8.0 0-16	14.8 9-20	9.8 4-16	24.5 18-28	32.5 27-41	22.4 0-44	20.8 15.0 17.8 92.1 17-24 9-24 14-24 85-100
Treatment C (16 crowded 4 hours)	\bar{X} 1.2 1-2	0.5 0-2	1.8 1-3	6.5 4-13	3.2 0-6	9.8 5-19	11.5 6-21	16.8 10-30	12.8 3.8 9.2 59.0 9-18 0-6 8-12 33-88
Treatment D (16 crowded 16 hours)	\bar{X} 4.8 1-10	8.2 0-17	13.0 3-22	9.8 7-14	11.2 3-19	21.0 13-27	34.0 30-39	37.6 10-63	16.2 22.0 18.8 89.6 15-17 13-26 15-20 78-100
F	1.40	1.41	2.10	3.25	1.99	2.62	10.52**	<1	3.51 8.52** 6.10* 4.51

used, the control and the most intense (16 aphids together for 16 hours). Because there were only 2 treatments in each of experiments 22, 23, and 24, t rather than F values were calculated.

In experiment 22, first instar larvae from uncrowded parents were raised to maturity individually. 8 were maintained separately as controls. 16 were crowded together for 16 hours, after which, they were again kept separately. The first several batches of offspring were collected and raised to maturity. 1 of the control parents and 2 of the treated parents did not survive long enough to produce offspring. The results are recorded in table 25. There was little difference between the 2 treatments in any of the measurements taken. The control group had the higher proportion of alatae.

The aphids used for experiment 23 were raised under conditions similar to those in experiment 22. Only 4 controls were used and of the 16 crowded together, 8 were selected as progenitors. The 16 aphids were crowded in the small cage. The use of the small cage increased the effective population density by a factor of 2.25. The results appear in table 25. As in experiment 22, none of the measurements made showed a significant difference between the controls and the treated individuals. Again, the controls had a greater percent alatae than the treated aphids.

Experiment 24 was identical to experiment 23 except that

Table 25

Number of alate and apterous offspring and average number of offspring per cage born to aptera crowded 16 together in the large or the small cage

<u>Experiment 22</u>		Total number alate offspring	Total number apterous offspring	Total number offspring reaching maturity	% alate	Average number of offspring per cage	% survival
Grand mean all treatments		21.2	43.0	64.2	32.7	17.6	94.0
Treatment A	\bar{X}	26.3	42.6	68.9	38.0	18.3	94.2
(control)	R	15-31	36-47	61-78	25-45	16-22	88-99
Treatment B	\bar{X}	18.7	43.2	61.9	30.0	17.3	93.8
(16 adults							
16 hrs in	R	5-31	25-59	50.72	9-55	16-20	81-100
large cage)							
t		0.01	0.63	0.44	1.02	0.29	0.15
<u>Experiment 23</u>							
Grand mean all treatments		9.0	18.9	27.9	31.2	15.5	90.9
Treatment A	\bar{X}	13.8	16.0	29.8	45.4	16.8	89.8
(control)	R	10-16	14-20	29-30	30-53	16-18	83-97
Treatment B	\bar{X}	6.6	20.4	27.0	24.2	14.9	91.4
(16 adults							
16 hrs in	R	2-12	16-26	20-33	7-37	12-18	84-97
small cage)							
t		0.36	0.27	1.29	2.54	0.26	2.40

the aphids were crowded in their fourth instar, rather than as newly emerged adults. Table 26 gives the results. There is a significant difference in the proportion of alatae between the controls and the treatment parents, the treated having a greater percent alatae. The greater proportion of alatae was a consequence of both more alatae in the treated and more apterae in the untreated group. The other significant factor was the size of the offspring group in the second batch. It was larger for the treated group and therefore the postnatal effects could not be ruled out as a cause for the increased alate production.

b. Larvae. The results of experiments 25, 26, 27 are given in table 28. Crowding first instar larvae of comparatively uncrowded parents at a density of 16 per 50.2 mm did not result in proportionately more becoming alate than among the uncrowded control individuals. In experiment 26, where the parents were raised individually for most of their lives, the difference in the proportion of alatae between crowded and uncrowded larvae appeared to be more definite, perhaps because the crowding was twice as severe as in experiment 25. The more intensive crowding of the treated individuals in experiment 27 resulted in a still larger proportion becoming alate. The effects of heavy parental crowding were apparently reversed in the control individuals.

4.0 General discussion

A few observations that transcended the 3 general types of experiments were made and their discussion has been reserved for

Table 26 Experiment 24

Number of alate and apterous offspring and average number of offspring per cage born to aptera crowded 16 together for 4 hours in their fourth instar

	Number of alate offspring		Number of apterous offspring		% alate	Average number of offspring per cage		% sur- vival			
	first batch	second total batch	first batch	second total batch		first batch	second total batch				
Grand mean all treat- ments	2.8	4.2	6.9	14.1	15.1	29.2	18.3	18.2	21.8	20.1	90.4
Treatment \bar{X} A (control) R	1.8	0	1.8	15.2	17.8	33.0	4.9	18.5	20.0	19.5	90.5
	0-6	0	0-6	12-18	17-19	30-37	0-17	16-22	19-21	18-22	84-95
Treatment \bar{X} B (16 crowded 4 hrs.) R	3.2	6.2	9.5	13.5	13.8	27.2	25.0	18.1	22.8	20.4	90.4
	0-10	0-21	0-23	10-16	7-23	18-33	0-49	16-21	14-36	15-27	78-100
t	0.32	2.28	1.62	0.65	1.54	0.36	2.96*	0.73	2.68*	0.56	0.85

* = $P < .05$

Table 27

Description of experiments 25, 26, 27

Experiment number	Number of replicates	List of treatments	Description of treatments	Parental environment
25	8	A	Control- 16 hrs. away from plant, individually in small cages	relatively uncrowded
	16	B	Treated- 16 hrs.; 16 together in a small cage, away from plant (16 per 50.3 mm ²)	
26	8	A	Control- same as experiment 25	uncrowded
	16	B	Treated- 32 together for 16 hrs. in small cage away from plant (32 per 50.3 mm ²)	
27	8	A	Control- 8 kept individually for 24 hrs. away from plant	crowded
	48	B	Treated- 48 together for 24 hrs. in small cage, away from plant (48 per 50.3 mm ²)	

Table 28

χ^2 for independence between crowded and uncrowded larvae, and development into the apterous or alate state

Experiment 25	Apterous		Alate		O-T	(O-T)
	O	T	O	T		T
Control	3	2.25	2	2.75	.75	.25
Treated	6	6.75	9	8.25	.75	.21
					.75	.08
					.75	.07
						$\chi^2 = .61$

Experiment 26	Apterous		Alate		O-T	(O-T)
	O	T	O	T		T
Control	6	4.29	0	1.71	1.71	.68
Treated	9	10.71	6	4.29	1.71	1.71
					1.71	.27
					1.71	.69
						$\chi^2 = 3.34$

Experiment 27	Apterous		Alate		O-T	(O-T)
	O	T	O	T		T
Control	6	3.3	0	2.7	2.7	2.21
	10	12.7	13	10.3	2.7	2.70
					2.7	.57
					2.7	.71*
						$\chi^2 = 6.19^*$

O = observed T = theorethical * = $P < .05$

the general section here presented.

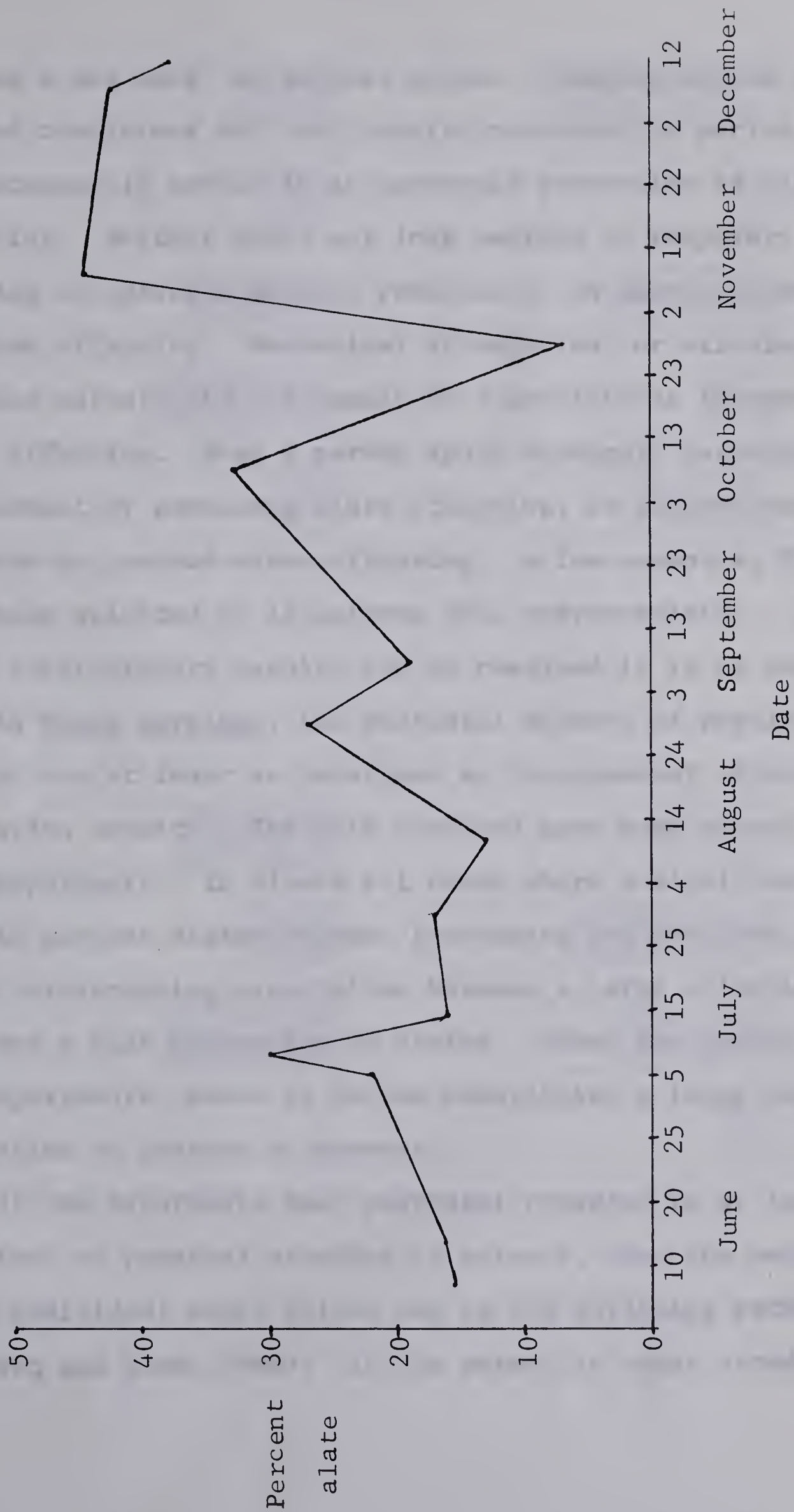
There was some merit in considering the long term tendency with respect to alate production. Fig. 2 is a plot of the percent alate of control treatments against time. The variation was considerable and there was no discernible long term trend. Bonnemaïson (1951) found that over a 6 month period during which he experimented with M. persicae, there was a general tendency for increased alate production with increased age of the clone. This was not so in my experiments over the period June through December.

No matter how careful I was to keep a parent isolated from other adults during both its infancy and adulthood, I was never able to prevent completely the occurrence of some alatae among its offspring. Fig. 2 illustrates the point. Never were the offspring of control parents entirely apterous. This implies that the production of a small proportion of alatae may be obligatory in M. persicae in the clone studied.

The rate of survival of offspring was high in all of the experiments. The average survival rate was 88.1 percent over all the experiments. An exception was the larvae which were stroked during their first and second instars, many of which died before reaching maturity. The survival rate of the parents was also high. Only 14 of 421 died before leaving a significant number of offspring.



The results I have obtained differ from Bonnemaïson's,

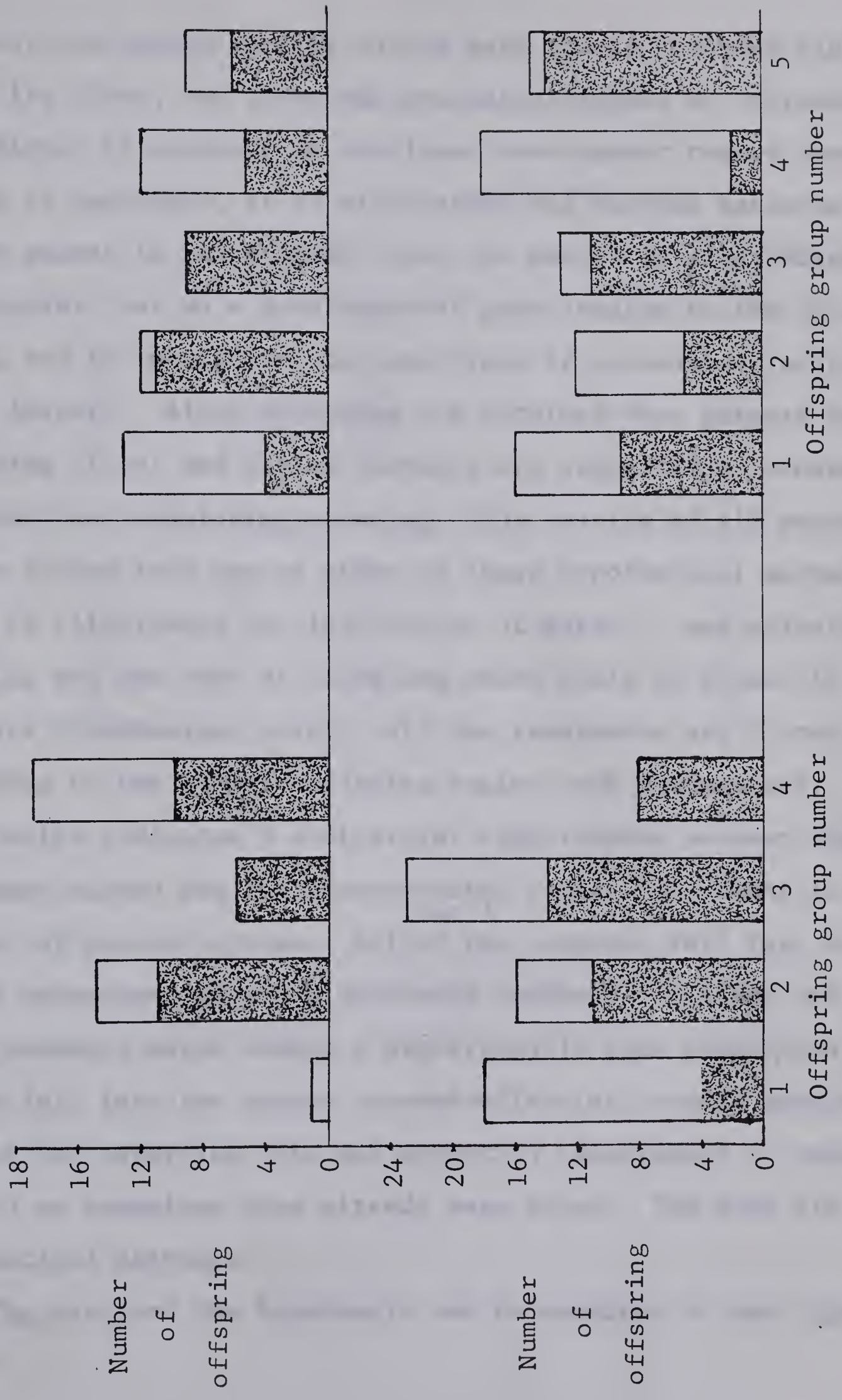
Fig. 2 Percent alate in control treatments for June to December



Johnson's and Lees' on several points. Rearing aphids under crowded conditions for their entire reproductive period did not necessarily result in an increased proportion of alate offspring. Neither short nor long periods of temporary crowding of apterous parents resulted in an increased proportion of alate offspring. Mechanical stimulation, or stroking, of apterous parents did not result in a predictable increase in alate offspring. When a parent aphid seemingly responded to a treatment by producing alate offspring, it did not necessarily continue to produce alate offspring. A few examples, Fig. 3, have been selected to illustrate this characteristic. All of these contradictory results can be resolved if it is assumed that in Myzus persicae, the postnatal effects of population density are at least as important as the prenatal effects of population density. The data obtained gave much support to this hypothesis. In almost all cases where a significant difference in percent alatae between treatments was obtained, there was a corresponding association between a large offspring group size and a high proportion of alatae. Under the conditions of the experiments, about 15 larvae constituted a large enough population to produce a response.

If the hypothesis that postnatal crowding is at least as important as prenatal crowding is correct, then the ontogeny of an individual would follow one of the following pathways (Johnson and Birks 1960): if the parent is under crowded con-

Fig. 3 Numbers and the ratio of alate to apterous offspring in consecutive batches born to individual parents of M. persicae  alate  apterous



ditions, the embryo remains on the path toward becoming alate. After its birth, the larva may encounter crowded or uncrowded conditions; if crowded, it continues development toward becoming alate; if uncrowded, it is sidetracked and becomes apterous. If the parent is not crowded, then the embryo is sidetracked and irreversibly set on a developmental path leading to the apterous state, and is insensitive to conditions it encounters in its early instars. Alate offspring are obtained when parents and offspring (first and second instars) are subjected to crowding or conditions simulating crowding. The results of all experiments can be fitted into one or other of these hypothetical pathways. Table 29 illustrates the interaction of parent and offspring crowding and the type of offspring which would be formed if the pathways hypothesized exist. All the treatments are listed according to the parent offspring regime each encountered. An asterisk indicates a statistical significance between the treatment marked and the corresponding control treatment in respect of percent alatae. All^{but 1}/of the controls fall into the parent uncrowded-offspring uncrowded quadrant. All but one of the treatments which showed a significantly high proportion of alatae fall into the parent crowded-offspring crowded quadrant. Reasons for regarding this one exception (experiment 5, treatment C) as anomalous have already been given. The data fit the hypothetical pathways.

The data and the hypothesis can be examined in the light

Table 29

Treatments listed according to parent-offspring
crowding encountered

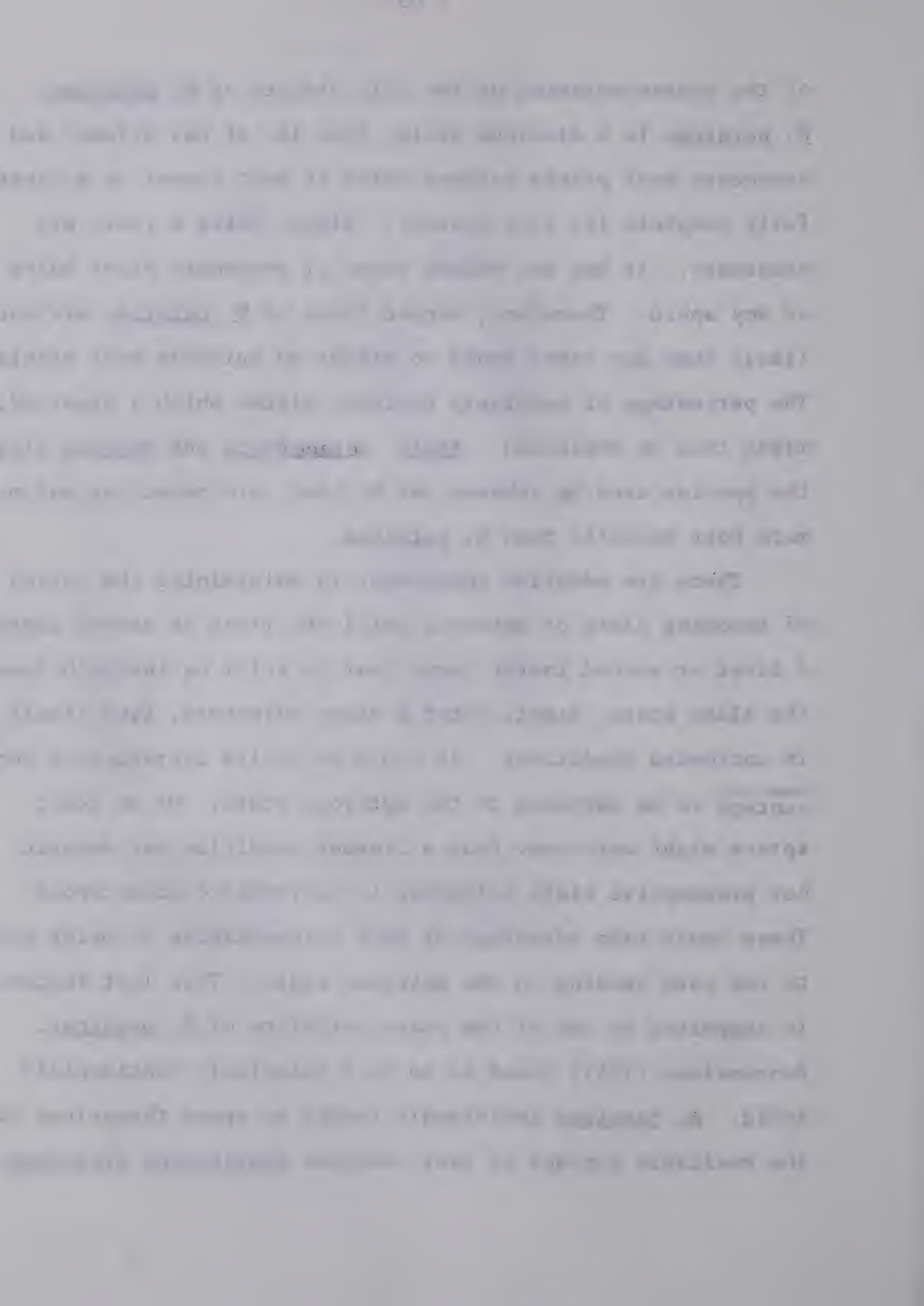
		Parent	
		Crowded	Uncrowded
		Form expected: alate	Form expected: apterous
Offspring	Crowded	1B* 4D* 1C* 4E* 2B 4F* 2C* 24B* 4C 27B*	11B 14B-D 11C 19A-D? 12B 25B 12C 26B 13A-C
	Uncrowded	Form expected: apterous	Form expected: apterous
		3B 8A-C? 3C 9B-D? 5A? 10A-C? 5B? 17B 5C* 17C 6B 20A-D? 6C? 21A-D 6D? 22B 7A-C? 23B	1A 12A 2A 13D 3A 14A 4A 17A 4B 18A-D 5D 22A 6A 23A 7D 24A 8D 25A 9A 26A 10D 27A 11A

* = statistical difference between treatment
marked and corresponding control in alate
production

? = treatment assumed to simulate crowding

of the characteristics of the life history of M. persicae. M. persicae is a diecious aphid, that is, it has primary and secondary host plants between which it must travel to successfully complete its life history. Wings, twice a year, are necessary. It has the widest range of secondary plant hosts of any aphid. Therefore, winged forms of M. persicae are more likely than any other aphid to alight on suitable host plants. The percentage of seemingly obligate alatae which I observed, might thus be explained. Aphis craccivora and Megoura viciae, the species used by Johnson and by Lees, are monocious and much more host specific than M. persicae.

There are adaptive advantages to maintaining the option of becoming alate or apterous until the first or second instars. A first or second instar larva that is still on the path toward the alate state, might, after a heavy rainstorm, find itself in uncrowded conditions. It would be to its reproductive advantage to be switched to the apterous state. Or an adult aptera might walk away from a crowded condition and deposit her presumptive alate offspring in uncrowded circumstances. These could take advantage of such circumstances by being shunted to the path leading to the apterous state. This last instance is supported by one of the characteristics of M. persicae. Bonnemaison (1951) found it to be a relatively "antisocial" aphid. M. persicae individuals tended to space themselves over the available surface of leaf, whereas Brevicoryne brassicae L.,



a more sociable type, remained in family groups.

5.0 Conclusion

The higher the population density of the parents, the greater is the proportion of alate offspring born to apterous Myzus persicae Sulz. But this general tendency can be overcome by preventing the size of the offspring groups from becoming too great. Apteræ raised on cabbage produced a greater proportion of alate offspring than apteræ raised on radish. The percent survival of offspring reared on radish was high, near 90; on cabbage was lower, near 70. The fecundity of parents fed on cabbage was less than that of parents fed on radish. The fecundity and longevity of singly reared parents did not differ from that of parents reared in groups. No association between the physiological age of the parents and the tendency to produce alatae was observed.

An attempt was made to imitate physical contact among aphids by stroking individuals. Stroking adult, apterous aphids on the dorsal surface with a Drosophila leg or a human hair, at intensities of 100 or 300 strokes per day was ineffective in causing the aphids to produce alate offspring. Stroking particular parts of the body, with an aphid leg, at intensities of 400 or 500 strokes per day was also ineffective. Areas stroked included the head, thorax, fore and hind parts of the abdomen, the sides of the abdomen, the antennae and the legs. Stroking applied generally to the entire dorsal surface at 300 or 1000

strokes per day may have caused a slight increase in alate production. 100 strokes daily applied generally over the dorsal surface elicited a highly significant increase in the number of alate offspring. However, this result may have been anomalous. 2 or 5 minutes daily contact of adult apterae with other adults mounted live on a pin, caused a slight increase in the proportion of alate offspring born to them. There was an association, across the treatments of the stoking experiments, between a large number of offspring per cage and a large proportion of alate offspring.

Stroking first and second instar larvae at intensities of 200, 300 or 500 strokes once or twice per instar did not cause these larvae to develop into alatae. Offspring of these larvae were not disproportionately alate.

Starving young, adult apterae for short periods (up to 16 hours), did not affect the number of alate offspring produced. Crowding young, adult apterae at population densities up to 16 per 50.3 mm² for up to 16 hours did not result in an increased number of alate offspring. Crowding first instar larvae whose parents had been crowded, resulted in an increased number of them becoming alate in the clone studied.

In Myzus persicae the first instar larvae as well as their parents must be crowded before there is an increase in the number of alate individuals produced. The capacity to be channelled into the developmental pathway leading to the apterous state is

retained beyond the embryo stage and well into the first and possibly second instars in the clone studied.

6.0 References

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